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Physiological side-effect model for diversification of non-functional or neutral traits: a possible evolutionary history of *Vanessa* butterflies (Lepidoptera, Nymphalidae)

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Abstract Butterfly wing color-patterns are highly diverse. Many color-patterns or their elements are ecologically and behaviorally functional in mating, mimicry and camouflage, but it has been thought that not all of them have clearly identifiable functions. How such non-functional, sometimes extravagant color-pattern traits evolved has been enigmatic. To illustrate this process, a model for the color-pattern evolution of the Admiral butterflies (the genus *Vanessa sensu stricto*) is proposed. It is first assumed that ancestral populations of *Vanessa* were geographically isolated in high altitude regions where temperatures fluctuate widely. In this model, pupae produce the cold-shock hormone (CSH) to protect differentiating cells in response to the temperature fluctuation. This hormone has an opportunistic ability to modify the wing color-patterns as a side effect or pleiotropic effect, revealing phenotypic plasticity of the ancestral populations. The modified phenotypes are rarely adaptive; they are in most cases either not favorable in mating or simply neutral with no adverse or adaptive effects. The modified phenotypes are nonetheless canalized in a population through a process of genetic assimilation accompanying natural selection for high hormonal activity, resulting in diverse orange areas on the wings in the present *Vanessa* species living in high altitude regions. Thus, the CSH physiologically acts as a mediator of genetic assimilation of the non-functional or neutral traits. In other words, a non-functional or neutral trait can be assimilated in a population as a "parasite" of a functional trait. Following the evolution of mating preferences, premating reproductive isolation might be established, as in the classical mechanism for allopatric speciation. This "physiological side-effect model" may explain the non-functional or neutral wing color-pattern diversity of *Vanessa* and other butterflies.

Key words Lepidoptera, Nymphalidae, *Vanessa*, color-pattern evolution, phenotypic plasticity, genetic assimilation, pleiotropy, speciation, cold shock, non-functional trait, neutral trait.

Introduction

The variety of butterfly wing color-patterns function as visual signals for mates or predators, and accordingly, many of them are important traits for natural selection (Uesugi, 1991; Jiggins *et al.*, 2001; Kapan, 2001). In some species of butterflies, subtle color-pattern differences between individuals are visually discriminated (Fordyce *et al.*, 2002; Robertson and Monteiro, 2005), but in other species, only their rough patterns, but not detailed patterns, are thought to be functional as mating signals (Tinbergen *et al.*, 1942; Silberglied and Taylor, 1973; Hidaka and Yamashita, 1975; Rutowski, 1977; Wiernasz, 1989).

Accordingly, it has been thought that not all of the wing color-patterns or their elements are equally functional or adaptive. Some of the butterfly wing color-patterns or their elements appear to be non-adaptive, and in certain cases, they could be simply extravagant. Vivid illustrations of such cases can be found in seasonal polyphenism: its adaptive significance is only marginally known so far (Shapiro, 1976; Nijhout, 1991) although it is possible that unproven function might simply indicate incomplete knowledge of the adptive significance. It is the common view that the color pattern of a given species is a product of historical chance and biological necessity woven by natural selection and other factors.

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From the viewpoint of developmental biology, the mechanism of the eyespot formation on butterfly wings has been investigated extensively with surgical, physiological, and molecular biological techniques (Nijhout, 1984, 1991; French & Brakefield, 1992, 1995; Brakefield & French, 1995; Brakefield *et al.*, 1996; McMillan *et al.*, 2002; Monteiro *et al.*, 2006). There is much experimental data indicating that an eyespot focus on wings works as an organizing center for the color-pattern development, although the exact nature of the positional signal emerging from it is still largely enigmatic. The same organizing center seems to organize the pupal wing cuticle spot (Otaki *et al.*, 2005*a*). In addition, the color patterns may be determined not only by the putative positional signal from organizing centers but also by the cellular ability to interpret the positional signal, which could be modified by more systemic factors such as ecdysteroids (Koch & Bückmann, 1987; Koch *et al.*, 1996; Rountree & Nijhout, 1995) and the putative cold-shock hormone (CSH) (Otaki, 1998, 2003, 2007*a*; Otaki & Yamamoto, 2004*a*; Otaki *et al.*, 2005*b*).

I have been interested in the mechanism of wing-wide color-pattern determination during development and its relations to butterfly color-pattern evolution and speciation. Here I discuss how non-functional or neutral color-pattern traits evolved in butterflies. To illustrate the process, I focus on the Admiral butterflies, the genus *Vanessa* Fabricius, 1807 *sensu stricto*, which is now composed of nine species in total (Wahlberg *et al.*, 2005; Otaki *et al.*, 2006*a*; Vane-Wright & Hughes, 2007). Molecular phylogenetic analysis has revealed that the genus *Vanessa sensu stricto* can be divided into two groups: the *indica* group and the *atalanta* group (Otaki *et al.*, 2006*a*) (Fig. 1A). Furthermore, we have previously pointed out that one can arrange these *Vanessa* species, but not closely-related species of genera *Cynthia* Fabricius, 1807 and *Bassaris* Hübner, 1821 (although *Cynthia* and *Bassaris* are no longer formally valid as genera according to Wahlberg *et al.* (2005)), in a progressive linear series of the color-pattern differences mainly based on the quantitative value of "the relative area of orange (RAO)" on the dorsal forewings (Otaki & Yamamoto, 2004*b*) (Fig. 1B). Intriguingly, a similar color-pattern series is known to be induced by systemic injections of sodium tungstate into pupae of *Vanessa indica* (Herbst, 1794) (Otaki & Yamamoto, 2004*a*) (Fig. 1B).

The color-pattern phenocopies mentioned above are an experimental expression of phenotypic plasticity that is usually hidden in *V. indica*. Recent resurgent interest in phenotypic plasticity and ecological speciation in evolutionary biology (West-Eberhard, 1989, 2003; Scheiner, 1993; Pigliucci & Murren, 2003; Rundle & Nosil, 2005; Pigliucci *et al.*, 2006; Price, 2006) could make the *Vanessa* genus an important case of plasticity-related evolution. Indeed, I have already shown that the evolution of *Vanessa kershawi* (McCoy, 1868) is highly likely to have been triggered by a plasticity-related mechanism (Otaki, 2007*b*).

Following a brief overview of the color-pattern modifications of *Vanessa*, I propose a possible scenario for the color-pattern evolution of *Vanessa* butterflies, based on the fact that the color patterns of several *Vanessa* species are similar to those of *V. indica* induced by cold shock and other perturbations (Fig. 1). This "physiological side-effect model" explains not only the color-pattern diversity of *Vanessa* butterflies but also of other butterflies that harbor many non-adaptive, non-functional neutral traits. Such non-functional and neutral traits that accompany and even feature many species might have emerged similarly to this model. Although this model has not been proven yet, it is intended to construct a theoretical framework for future research. I also point out here that this model does not suggest an exclusive means, and other mechanisms may have been responsible for the color-pattern diversity of the genus *Vanessa sensu stricto* (Otaki, 2008). Some ideas presented here were already mentioned in Otaki *et al.* (2006*b*) in Japanese.

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The putative CSH and its physiological effect

It has been known that the color patterns of butterfly wings can be modified by the application of cold shock to pupae immediately after pupation (Nijhout, 1984; Shapiro, 1984). The patterns are not randomly modified, but there is a clear and consistent tendency: many color-pattern elements become obscure and some elements are erased or dislocated. In *Vanessa cardui* (Linnaeus, 1758), the black spots on the forewings become smaller or weaker (Nijhout, 1984; Shapiro, 1984). Although the response to the cold shock varies from individual to individual, the modified patterns can be arranged from less severe to highly severe in a linear fashion (Nijhout, 1984). In contrast, a non-linear response was seen in heat-shocked butterflies (Otaki, 2007*a*, *b*). This is an important point to consider, because cold-shocked-induced phenocopies, but not heat-shock-induced phenocopies, are suggested to be caused by a single mechanism.

Is this type of modification mediated by a hormonal factor that is secreted in response to cold shock? Alternatively, is it the scale cells themselves that directly respond to cold shock without any hormonal factor? To resolve this problem, Otaki (1998) performed hemolymph transfer from cold-shocked to non-cold-shocked individuals, and found that the modification-inducing property can be transferred, although the induced modifications in the recipients were relatively mild. The recipients showed dislocation of one of the color-pattern elements, the parafocal elements, toward the border ocelli (eyespots), reduction of black spots (hence expansion of the orange area), and other modifications as seen in cold-shocked individuals (Otaki, 1998). The existence of the putative CSH was then proposed in the literature. It was also proposed that the CSH functions to change the threshold levels for the putative morphogen without affecting the morphogenic positional information itself (Otaki, 1998).

The chemical nature of the CSH has not yet been established. However, if a hormonal factor is operating in the cold-shocked individuals, it may be relatively easy to phenotypically mimic the CSH effect by means of foreign chemicals including structural analogs that serve as a ligand (agonist or antagonist) for its receptor. The first "cold-shock agonist" discovered was sodium tungstate (Na_2WO_4), a supposed protein-tyrosine phosphatase inhibitor (Otaki, 1998). When injected into pupae, this chemical and also related ones, sodium molybdate (Na_2MoO_4) and molybdic acid (H_2MoO_4), induced pattern modifications that were indistinguishable from the cold-shock-treated one (Otaki, 1998; Otaki & Yamamoto, 2004*a*) (Fig. 1B). Tungstate and molybdate are likely to be highly stable in pupae because of their simple chemical structures. This modification-inducing ability of tungstate is shown to be largely specific to the color-pattern development, and such modifications are not observed with injections of stress-inducing chemicals such as urea (Otaki, 1998), thapsigargin, ionomycin, and geldanamycin (Otaki *et al.*, 2005*b*). The pharmacological effect of tungstate is thus considered as a functional mimic of the putative CSH (Otaki, 1998; Otaki *et al.*, 2005*b*). Totally different chemicals, a crude fungal extract (Umebachi & Osanai, 2003) and heparin and its related chondroitin sulfates (Serfas & Carroll, 2005), were then discovered to exhibit a similar effect. Also recently discovered were the "cold-shock antagonists", which induce modifications in the "reverse direction" (Serfas & Carroll, 2005; Otaki, 2007*a*) (Fig. 1B). Each of these agonists and antagonists probably affects a distinct and different point in the same molecular pathway for the development of the color patterns on the wings.

Although it is difficult to establish the molecular identity of the CSH in these physiological studies, these experiments revealed how and to what degree the butterfly color-patterns are plastic to external perturbations. Importantly, the linear arrangement of the modification-in-

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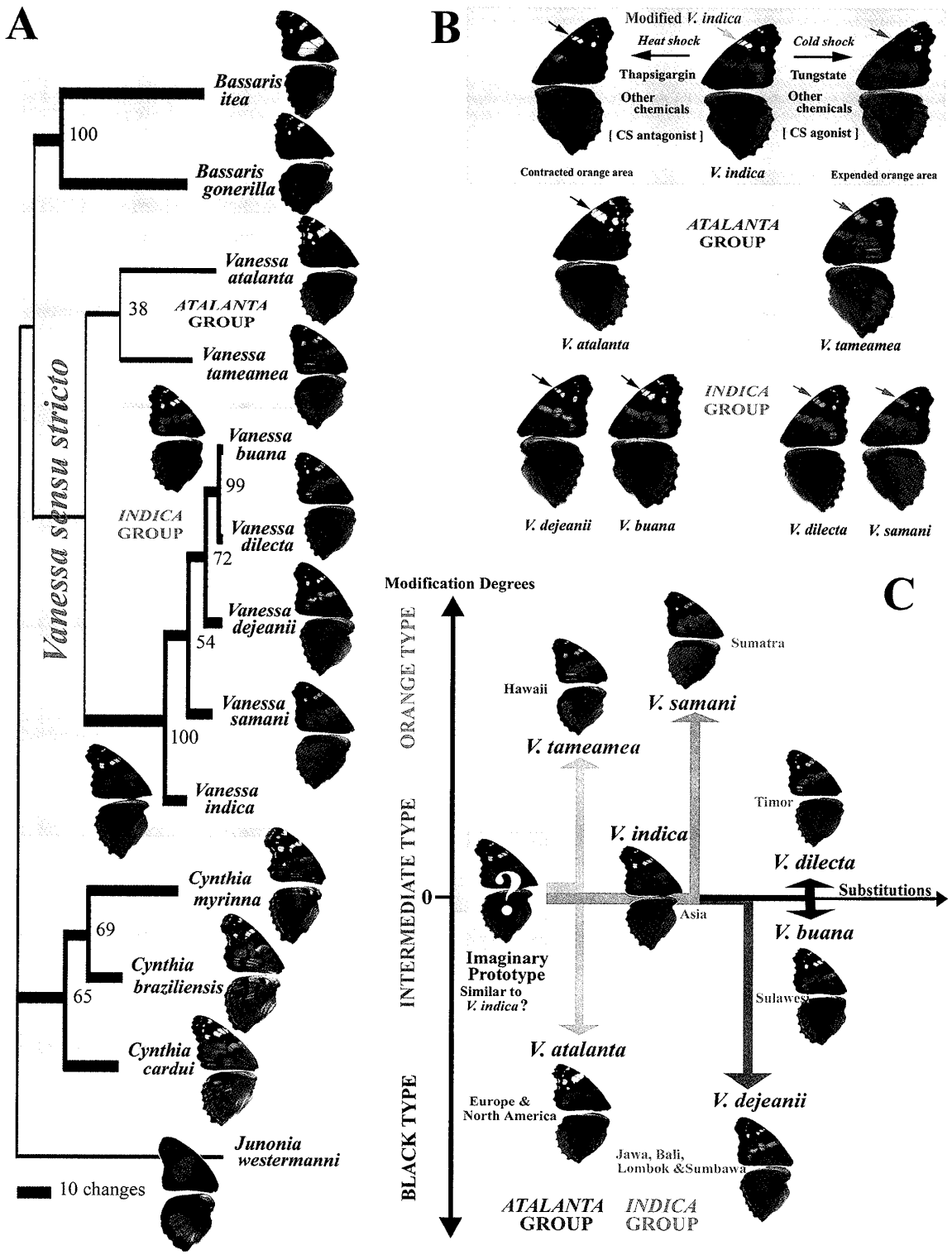

Fig. 1. Modified and normal color-patterns of *Vanessa* and their evolutionary implications. (A) Molecular phylogeny of *Vanessa* and its related genera (subgenera) based on the mitochondrial *ND5* (*NADH dehydrogenase subunit 5*) and *COI* (*cytochrome oxidase subunit I*) genes. Modified from Otaki *et al.* (2006*a*). A maximum parsimony (MP) tree diagram with bootstrap support is shown. Thick lines indicate clades with at least 50% bootstrap support. Monophyly of the *indica* group is clearly demonstrated. The *atalanta* group is also likely to be monophyletic. Although monophyly of *Vanessa sensu stricto* is not shown in this analy-

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duced *V. indica* individuals is reminiscent of that of normal *Vanessa* species based on the quantitative value of the relative area of orange (RAO) on the dorsal forewings (Otaki & Yamamoto, 2004*b*) (Fig. 1B).

In this normal species series, I noticed that the color of the subapical band embedded in the black apical area is either orange (*V. samani* (Hagen, 1895), *V. dilecta* Hanafusa, 1992, and *V. tameamea* Eschscholz, 1821 [although it is sex-dependent in *V. tameamea*]) or white (*V. dejeanii* Godart, 1824, *V. buana* (Fruhstorfer, 1898), and *V. atalanta* (Linnaeus, 1758)) except in *V. indica* whose subapical band has both white and orange scales (Fig. 1B). The color of the subapical band thus may be a useful trait to distinguish the evolutionary tendency of expansion or shrinkage of the orange area in *V. dilecta* and *V. buana*, whose orange area is not appreciably different from that of *V. indica*. Furthermore, the subapical band of the *V. indica* individual with the expanded orange area induced by experimental treatments is orange, although the band is compromised in shape. On the other hand, the subapical band of the *V. indica* individual with the contracted orange area induced by experimental treatments seems to be whiter than that of the normal individual (Otaki, unpublished data).

The subapical color of the modified individuals, in addition to the relative area of orange, thus faithfully recapitulates the normal series of *Vanessa* species. Hence, there is a possibility that *Vanessa* species evolved by taking advantage of phenotypic plasticity of their common ancestral species that has been retained in *V. indica* and that can be revealed by physi-

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sis, it is suggested by Wahlberg *et al.* (2005) and Field (1971). (B) Color patterns of the modified *V. indica* and the normal *Vanessa* species. The top pink panel shows the normal *V. indica* (middle), the modified *V. indica* induced by cold shock or its phenotypically equivalent chemicals such as tungstate (right), and the modified *V. indica* induced by heat shock or its phenotypically equivalent chemicals such as thapsigargin (left). The heat-shock and thapsigargin-injection experiments were published in Otaki (2008). The subapical band embedded in the black area at the apex in *V. indica* (purple arrow) is white with a small orange area. The color of this subapical band in a given species correlates with the relative area of orange (see below). This modified color-pattern series is reminiscent of the normal species series shown in the middle and bottom panels. The middle yellow panel shows four species that are molecular phylogenetically classified as the *indica* group excluding *V. indica* itself (Otaki *et al.*, 2006*a*). Compared to *V. indica*, *V. samani* shows a larger orange area and smaller black area together with an orange subapical band (orange arrow), whereas *V. dejeanii* shows a smaller orange area and larger black area together with a white subapical band (black arrows). Two species, *V. dilecta* and *V. buana* do not show appreciably larger or smaller orange areas, compared to *V. indica*, but they have either orange or white subapical bands (orange arrow and black arrow, respectively). The bottom blue panel shows two species that are molecular phylogenetically classified as the *atalanta* group (Otaki *et al.*, 2006*a*). Here again, *V. tameamea* has a relatively large orange area and small black area together with the orange apical band (orange arrow), whereas *V. atalanta* has a relatively small orange area and large black area together with the white apical band (black arrow). (C) Schematic diagram of the possible bi-directional color-pattern evolution of *Vanessa* species. The molecular phylogenetic analysis indicated that they are separated into two groups: the *atalanta* group and the *indica* group (Otaki *et al.*, 2006*a*). The color-pattern analysis indicated that they can be classified into three types: the orange type, the intermediate type, and the black type (Otaki *et al.*, 2006*a*). From the hypothetical prototype, which was probably similar to *V. indica* in terms of the wing color-pattern, at least four species, *V. tameamea*, *V. atalanta*, *V. samani* and *V. dejeanii*, independently and allopatrically increased or decreased the orange area on the forewings. Other three species, *V. indica*, *V. dilecta*, and *V. buana*, basically retained the ancestral color-patterns.

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ological experiments (Otaki & Yamamoto, 2004*b*). It is worth noting that the possible evolutionary importance of phenotypic plasticity in butterfly color-patterns has also been pointed out in a study of seasonal polyphenism (Shapiro, 1976).

Thus far, the site of action of the cold-shock agonists or antagonists has not been conclusively determined. Circumstantial evidence suggests that both neurosecretory cells and scale cells may be affected by cold shock, and the scale cells are likely to be affected by the cold-shock agonist or antagonist injections (Otaki, 1998; Otaki, unpublished data), but a different group proposed neurosecretory cells as an exclusive target (Serfas & Carroll, 2005). More studies are necessary to resolve this issue.

Species relationships and the color-pattern variation

Molecular phylogenetic results (Wahlberg *et al.*, 2005; Otaki *et al.*, 2006*a*) together with synthetic morphological analyses (Field, 1971) help us to decipher the possible evolutionary history of the classical genus *Vanessa sensu stricto*. In Otaki *et al.* (2006*a*), seven species of *Vanessa* were analyzed excluding *V. vulcania* Godart, 1819, which was previously recognized as a subspecies of *V. indica* (Field, 1971; Leestmans, 1978), and *V. abyssinica* (Felder & Felder, 1867), which was previously recognized as *Antanartia abyssinica* (Wahlberg *et al.*, 2005) and whose taxonomic position in *Vanessa* needs to be solidified by further integrative studies. This paper hereafter also focuses on these seven species of the genus *Vanessa sensu stricto*.

There are phylogenetically two groups in *Vanessa*: (1) the *atalanta* group, composed of *V. atalanta* and *V. tameamea*, and (2) the *indica* group, composed of the rest of the *Vanessa* species (Otaki *et al.*, 2006*a*). The phylogenetic tree of the *indica* group is shown as *V. indica* (*V. samani* (*V. dejeanii* (*V. dilecta* + *V. buana*))) (Fig. 1A). The monophyly of the *indica* group is clearly demonstrated. The *atalanta* group is also likely to be monophyletic, although not strongly supported. The molecular phylogenetic analyses by ourselves and other researchers (Wahlberg *et al.*, 2005; Otaki *et al.*, 2006*a*) are basically compatible with the synthetic morphological analyses of Field (1971).

In contrast, the color-pattern phenotype of the genus *Vanessa* can be classified into three types largely based on the relative area of orange (RAO) on the dorsal forewings: (1) the orange type, whose orange area is relatively large, *i. e. V. tameamea* and *V. samani*, (2) the black type whose orange area is relatively small, *i. e. V. dejeanii* and *V. atalanta*, and (3) the intermediate type, *i. e. V. indica*, *V. buana*, and *V. dilecta* (Otaki *et al.*, 2006*a*). This area of orange in *Vanessa* is slightly but significantly different from species to species (Otaki & Yamamoto, 2004*a*). To be sure, other color-pattern traits are also affected by the CSH and may be considered for a similar grouping purpose, but the orange area on the dorsal wings is the most conspicuous at least to human eyes and probably also to the eyes of *Vanessa* butterflies based on the molecular and behavioral data (Zaccardi, *et al.*, 2006). It is to be noted also that there is no conspicuous sexual dimorphism in the *Vanessa* species.

The functional significance of the orange area has not been strictly examined in *Vanessa*. However, it is known that *V. indica* primarily uses color visual cues rather than olfactory cues for flower visitation (Ômura & Honda, 2005), indicating the functional importance of the visual system in this butterfly behavior. Interestingly, *V. atalanta* cannot discriminate colors with long wavelengths, between yellow (590 nm) and red (620 nm), although it can do well between blue (440 nm) and yellow (590 nm) (Zaccardi *et al.*, 2006), indicating that *V. atalanta* and probably also other species of *Vanessa* recognize the color contrast (*i. e.* orange and black) but not the color itself in the long wavelengths of light. In a different

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nymphalid butterfly that has a similar broad orange stripe pattern with black background on the wings, *Yoma sabina*, an experimental study showed that the orange stripe with black background is important in the visual recognition (Warzecga & Egelhaaf, 1995). We can thus presume that the orange area on the dorsal forewings, when combined with a black background, produces high contrast, and this visual signal functions as a mating signal in *Vanessa*, despite the fact that *Vanessa* butterflies cannot recognize the orange color itself.

The combination of the phylogenetic and color-pattern analyses revealed an interesting trend (Otaki *et al.*, 2006*a*). The *indica* group contains one species of the orange type (*i. e. V. samani*), one species of the black type (*i. e. V. dejeanii*), and three species of the intermediate type (*i. e. V. indica*, *V. dilecta*, and *V. buana*). Likewise, the *atalanta* group contains two species with quite dissimilar color-patterns: one species of the orange type (*i. e. V. tameamea*) and one species of the black type (*i. e. V. atalanta*). This immediately indicates that the color-patterns based on the orange area do not simply reflect the molecular phylogenetic relations and the classification of Field (1971) based on genital and other morphological characters.

Such disagreement between the phylogenetic status and the color patterns is not surprising at all in butterflies. Butterfly color-patterns can be drastically different between closely-related species and even within a single species as exemplified by *Papilio dardanus*, *Papilio memnon*, and *Hypolimnas bolina* (Nijhout, 1991). Also color patterns can be very similar even between non-related species as seen in many pairs of mimics and their models. For these reasons, wing color-patterns are not considered as very useful traits for clarifying phylogenetic relations between butterfly species. This widely accepted fact straightforwardly indicates that the wing color-patterns of butterflies, not excluding *Vanessa*, have high degrees of freedom in development and evolution despite the existence of the nymphalid groundplan, which is the general framework for butterfly wing color-patterns (Schwanwisch, 1924; Süffert, 1927; Nijhout, 1991). The combined result of the phylogeny and the color-pattern analysis readily indicates that also in *Vanessa* even within a group of closely related relatives, the color-pattern can drastically vary. However, despite the color-pattern differences among species, the variation is always on the line of the simple color-pattern series: the expansion or shrinkage of the orange area.

Bi-directional color-pattern evolution

For the sake of discussion, here I would like to introduce a presumption that the ancestral species of *Vanessa* had a color pattern similar to *V. indica* (Otaki *et al.*, 2006*a*). This presumption, which does not contradict the molecular phylogenetic data (Wahlberg *et al.*, 2005; Otaki *et al.*, 2006*a*), is mainly based on the fact that *V. indica* occupies the middle position in the linear series of the quantitative color-pattern differences based on the RAO values (Otaki, *et al.*, 2006*a*). In addition, *V. indica* is widely distributed in Asia, indicating its genetic versatility to adapt itself to different environmental conditions, compared to other *Vanessa* species.

I believe that *Vanessa* speciation was a typical allopatric process, as proposed in Mayr (1942, 1963), because many of the present *Vanessa* species show restricted patchy distributions in isolated islands (Fig. 1C). Exceptions are *V. indica* and *V. atalanta*, both of which are distributed widely in the Eurasian (*V. indica* and *V. atalanta*) and North American (*V. atalanta*) Continents and are sister to island species. Thus, it is highly likely that the ancestral species was found on a continent and was closer to *V. indica* and *V. atalanta*. In the course of speciation, this hypothetical ancestral species was geographically isolated in a small island, and after many generations with no interbreeding with other populations of the

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ancestral species, genetic differences were accumulated in the isolated population, which eventually changed some traits that were related with sexual reproduction including the wing color-pattern. Four species, *V. tameamea*, *V. samani*, *V. atalanta*, and *V. dejeanii*, were differentiated with clearly appreciable expansion or shrinkage of the orange area (Fig. 1C), and the other three species, *V. indica, V. dilecta* and *V. buana*, simply retained a similar extent of the orange area and most of the color-pattern elements.

This "bi-directional" type of color-pattern evolution (*i. e.* expansion or shrinkage of the orange area) is clearly observed only within the genus *Vanessa sensu stricto*. It is not clearly observed in *Cynthia* or *Bassaris*. However, some nymphalid genera such as *Nymphalis* living in high altitude areas are likely to show similar evolutionary tendencies (Otaki, unpublished data). Interestingly, this tendency is seen irrespective of the two phylogenetic groups (*i. e.* the *indica* and *atalanta* groups) and also irrespective of geographical locations on the earth. Other than the change of the orange area, no drastic phenotypic evolution had happened in *Vanessa* such as the innovation of eyespots on the dorsal wings as seen in *Junonia* or the unequal expansion of eyespots on the ventral hindwings as seen in *Cynthia*.

It is true that *Cynthia* and *Bassaris* are also found in high altitude areas in tropical latitudes as well as in temperate areas. Why the bi-directionality is observed only in *Vanessa* but not in *Cynthia* and *Bassaris* is unclear at this point. But it would suffice to mention here that the direction of the phenotypic color-pattern divergence of species in *Vanessa* appears to be pre-determined as an evolutionary constraint at the genus level. In other words, this constraint is what characterize *Vanessa* and distinguish it from other genera.

Based on the discussion above, an explanation that this bi-directional tendency of the color-pattern changes is merely a product of random genetic drift or stochastic events that happened in each species independently with no pre-determined constraint cannot be justified. This evolutionary constraint being unique to *Vanessa* may have played an instructive role in the color-pattern evolution in *Vanessa*. Each differentiating population might have had the freedom to set the level of the orange in accordance with the environmental conditions (see below).

Although the possibility that the bi-directional color-pattern evolution might have been directly shaped by natural selection cannot be ruled out completely, it is at least equally reasonable to think that the small increase or decrease of the orange area was ecologically too trivial to be selected for in the early stages of the specific differentiation of *Vanessa*. It is to be noted that whether or not the present *Vanessa* species can discriminate the interspecific RAO differences does not either deny or support this idea.

To be sure, the orange area itself is likely to be behaviorally important as discussed above, but its small bi-directional modifications (*i. e.* increase or decrease of the orange area) would not be able to confer any ecological advantage on the ancestral species of *Vanessa*, even if the optimal width of the orange area may be behaviorally important in some of the present species of *Vanessa*. It is also important to notice that most, if not all, *Vanessa* species certainly evolved allopatrically, judging from their patchy distribution pattern in isolated islands (see above; Fig. 1C). In other words, the ancestral color-pattern would be just good enough for mating recognition in the isolated environment where no other closely related species existed. Furthermore, since there is no clear sexual dimorphism in color patterns in *Vanessa* (an exception is the subapical band color in *V. tameamea*), it can be concluded that sexual selection did not play a central role in the course of the specific differentiation of this genus, although an assortative mating process may be necessary to spread a particular genotype that supports one of the plastic phenotypes in the isolated population (see below; Fig. 2A).

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Physiological link with the cold-shock resistance

It can be argued as above that the origin of the interspecific RAO differences and hence the bi-directional color-pattern evolution cannot be reasonably found in its ecological and sexual functionality. This is not surprising in that not all butterfly color-patterns have clearly identifiable function at least to biologists. Rather, many butterfly color-patterns are simply extravagant with many non-functional pattern elements (see Introduction), and I believe that *Vanessa* is not an exception. Then, how did the bi-directional color-pattern evolution originate in *Vanessa*? To put it differently, what is the real factor behind the evolutionary constraint of the genus *Vanessa*?

To resolve this problem, the color-pattern evolution can be considered as a consequence of natural selection for a seemingly unrelated ecological trait. That is, in association with the evolutionary constraint or phenotypic plasticity discussed in the previous section, a novel color-pattern might have occurred as a by-product of the process of physiological selection for new environmental conditions in which the cold-shock or heat-shock events frequently occur. To put it differently, physiological or genetic changes for a new environment via natural selection might have caused the color-pattern modifications and evolution as a side effect, because of the opportunistic physiological link between the cold-shock resistance and the color-pattern modifications. This is consistent with the fact that the genus *Vanessa* is composed of species that are adapted to environmental temperature fluctuations in temperate area.

In this "physiological side-effect model" (Fig. 2A), an ancestral population is first exposed to a new environment with highly fluctuating temperatures. For the efficient protection of differentiating pupal cells against the environmental cold shock, the putative CSH is produced into the hemolymph. The ability to produce the hormone efficiently varies among individuals due to different genetic composition. The environment primarily selects individuals with high cold-shock resistance based on the efficient production of the CSH.

However, this hormone, if secreted during the formation of the wing color-pattern, has an opportunistic ability to modify the color-pattern determination process of scale cells, leading to the wing-wide color-pattern modifications of the individual. That is, as a side effect of this hormone, the wing color-pattern is modified, and as a result, the number of individuals with "aberrant" color-patterns increases in the isolated population. In other words, the morphological diversity within that population is promoted, as seen in a natural population of *Zizeeria maha* (Kollar, 1844) exposed to a new cold environment (Kudo & Ichida, 2002; Otaki & Kudo, unpublished data).

If the highly modified color-patterns are not attractive to mates (shown as (1) in Fig. 2A), the mating process negatively affects the selection step for the cold-shock resistance by not favoring the individuals with high hormonal activity. As a compromise, individuals with "appropriate" hormonal activity may survive better than those with high hormonal activity. The survivors may show relatively small but significant color-pattern modifications. This way, both the physiological phenotype (*i. e.* the cold-shock resistance) and its opportunistic phenotype (*i. e.* the modified color-patterns) as a by-product are genetically assimilated in the population.

Not all color-pattern modifications will have a negative effect on mating, because not all color-patterns or their elements can function as mating signals and in many butterflies only the rough patterns are thought to be functional (see Introduction). It would often be the case that the color-pattern modifications are not even recognized by mates, because of the

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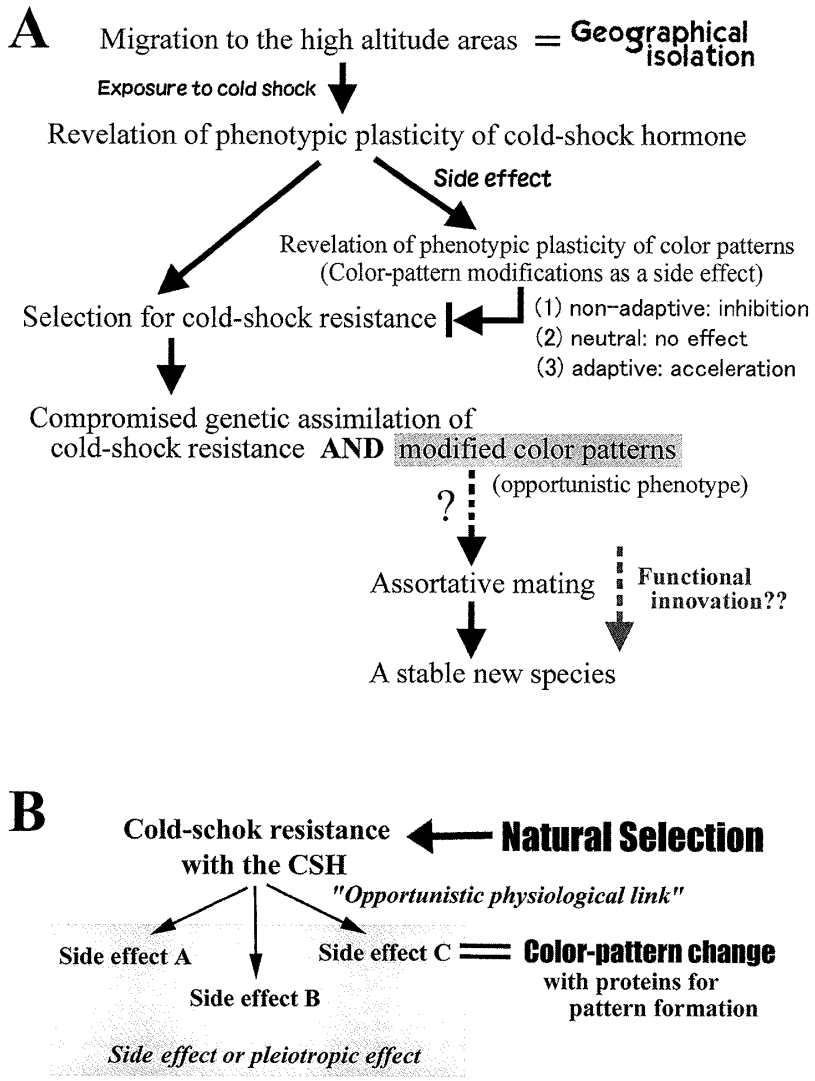

Fig. 2. Physiological side-effect model for the color-pattern evolution of *Vanessa* butterflies. (A) Evolution of *Vanessa* color-patterns. In this model, the ancestral population that migrated to high altitude regions is geographically isolated and exposed to natural cold-shock events. In response to the cold shock, the cold-shock hormone (CSH) is produced into the hemolymph. Phenotypic plasticity of hormone production may be revealed by this process. In addition, the produced hormone modifies the wing color-pattern as a side effect, although its primary function is to protect differentiating cells from cold shock. Here, phenotypic plasticity of the wing color-patterns is revealed, resulting in the phenotypically diverse population. At this point, three cases may be considered. (1) The produced modification may be non-adaptive. That is, the modified color-pattern is not attractive to mates, which inhibits the positive selection for cold-shock resistance. If highly adverse, the modification may entirely stop the selection step for cold-shock resistance, and such a population may die out. If not so adverse, this step may inhibit the selection only slightly, and the modification may accompany the evolution of cold-shock resistance. (2) The produced modification may be neutral with no adverse effects and no adaptive values. In this case, the modified color-pattern simply accompanies the selection for cold-shock resistance. (3) The produced modifications may be adaptive in rare cases. In that case, selection for the cold-shock resistance will simply be accelerated by the adaptive selection for the color pattern. In any case, if the population does not die out, the result is the genetic assimilation of the cold-shock resistance and the modified

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subtlety of the modifications or the limitations of the butterfly visual system (Takeuchi *et al.*, 2006; Kinoshita & Arikawa, 2007), even if the modifications are obvious to human eyes or morphometric analysis. Therefore, there is a significant chance that the modified phenotype or the side-effect of the hormone is functionally neutral with respect to natural selection (shown as (2) in Fig. 2A). In that case, the color-pattern modifications do not negatively affect the selection step, and thus, they are smoothly assimilated genetically in association with the cold-shock resistance that results from the efficient production of the hormone. Rarely, the modified pattern is more attractive than the original pattern (shown as (3) in Fig. 2A). But if it happened, the modified phenotype positively affects the selection process, and will be genetically fixed in the population.

Implications of the physiological side-effect model

The physiological side-effect model states that the cold-shock resistance was the main driving force in the evolution of these *Vanessa* species and that the color patterns did not evolve as the direct target of natural selection but did evolve as a result of a side effect (Fig. 2B). In other words, a non-functional or neutral color-pattern can be assimilated in a population as a "parasite" of a functional trait. The bi-directional color-pattern evolution is the evolutionary constraint of this genus, but mechanistically, it is accidental or secondary to the evolution of the cold-shock resistance. Therefore, it may be more appropriate to state that the evolutionary constraint of the genus *Vanessa* is not the bi-directional color-pattern itself but the physiological ability or tendency to spread into a new locality where temperature fluctuates widely. Resistance against high temperature fluctuations was probably inherent in the ancestral species of this genus, and secondarily determined the bi-directionality of the color-pattern evolution.

The CSH links the physiological selection process to the color-pattern determination process during development. Importantly, this "opportunistic physiological link" allows a neutral or even slightly unfavorable phenotype to be assimilated genetically. The linkage between the adaptive selection (or the CSH) and the color-pattern development (or proteins for pattern formation) is, in this case, physiological, and not necessarily genetic at first. Genes for the CSH and the color-pattern development may well reside in different places remotely in different chromosomes. That is, two groups of genes (*i. e.* genes for the CSH expressed in neurosecretory cells and genes for the color-pattern formation expressed in scale cells) do not have to be positioned side by side or physically close to each other in the same chromosome. Theoretically, any genes can be physiologically linked with the gene that codes for a hormone, making two or more traits evolve together.

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color-pattern together. This modification process may be then linked with an assortative mating process, which may eventually establish a stable new species with new physiological and morphological traits, *i. e.* cold-shock resistance and unique color-pattern. During the evolution of the mating preferences for the assortative mating, the new color-patterns may acquire new ecological or behavioral functions. (B) Relations between the cold-shock resistance (and the CSH expressed in the neurosecretory cells) and the color-pattern change (and proteins that are responsible for it expressed in scale cells). The cold-shock resistance is the direct target for natural selection. This selection results in its side effect or pleiotropic effect. But such an effect may not be singular but plural, shown as A to C in this diagram. Color-pattern change is shown as the side effect C in this diagram. The cold-shock resistance (and the CSH expressed in the neurosecretory cells) has physiological relation with the color-pattern change (and proteins that are responsible for it expressed in scale cells).

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The fact that most, if not all, cases of phenotypic plasticity studied well involve hormonal regulation in response to environmental conditions (Nijhout, 2003) is encouraging for the side-effect model, in which the CSH plays a central role. The putative CSH probably functions as an evolutionary capacitor, as general complex gene networks, exemplified by the heat-shock proteins (Rutherford & Lindquist, 1998; Queitsch *et al.*, 2002) and developmental hormones (Suzuki & Nijhout, 2006), appear to work as evolutionary capacitors for genetic variation (Bergman & Siegal, 2003). Accordingly, in this model, no new mutations have to be introduced during evolution. The new traits are thought to be "genetically stored" already without phenotypic expression through the capacitative function of the CSH, and its ability is simply released as phenotypic plasticity upon contact with new environments. The physiological side-effect model may also be applicable to other hormones such as ecdysteroids.

The side-effect model may be considered as a case of pleiotropy. Pleiotropy is known as the major brake of evolution, because in most cases an advantageous functional change in one trait could also cause an adverse effect on another trait (Barton, 1990; Otto, 2004). However, the pleiotropic effect can be exploited for cellular cooperation (Foster *et al.*, 2004) and is proposed to be responsible for the evolution of harmful behavior of males to females (Morrow *et al.*, 2003). It is tempting to speculate that butterfly wing color-patterns also exploit pleiotropy of genes including genes for the CSH for phenotypic diversification.

Intriguingly, some similarity to our model may be postulated in the allochronic reproductive isolation of a melon fly, in which natural selection for the function of clock genes causes several changes in phenotypic traits including reproductive ones due to the pleiotropic effect of the clock gene (Miyatake & Shimizu, 1999; Miyatake, 2002; Miyatake *et al.*, 2002). The side effect of the CSH may be considered as an example of pleiotropy of the gene that codes for a hormone (Fig. 2B). If the CSH affects not only the scale cells for color-pattern development but also reproductive organs accidentally through its pleiotropic effect, this may be a case that suggests a molecular mechanism of allopatric speciation based on the biological species concept. In that case, the physiological side-effect model could be efficiently connected to a process of speciation.

Although the side-effect model cannot propose a detailed mechanism for the process of butterfly speciation, we have found a case that could link the two. A pair of *Maculinea* butterflies, *Maculinea teleius* (Bergsträsser, 1779) and *Maculinea arionides* (Staudinger, 1887), found in high altitude mountainous regions, shows a color-pattern trend that is similar to the modified patterns of *Zizeeria maha* (Otaki & Yamamoto, 2003; Kudo & Ichida, 2002; Otaki & Kudo, unpublished data). Interestingly enough, in *Heliconius* butterflies, genes for mate preference and wing color-pattern development are identical or closely located in the genome, indicating that the evolution of color patterns directly accompany the evolution of mate preference (Kronforst *et al.*, 2006).

Although highly speculative, this model might suggest the importance of the pupal stage for the expression of phenotypic plasticity. The hormone modifies the developmental process of scale cells during pupal development, opportunistically linking ecological selection for cold-shock resistance and color-pattern development. This model, in which the pupal stage is important, is also consistent with the fact that insects with complete metamorphosis (*i. e.* Holometabola) have more species diversity than those with incomplete metamorphosis (*i. e.* Hemimetabola).

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Conclusions

I here show a possible scenario for the evolution of *Vanessa* butterflies with special reference to their color-pattern diversity. This model proposes a novel mode of evolutionary mechanism: a physiological side effect as an important factor for phenotypic evolution, especially for neutral or even slightly unfavorable phenotypic traits. The CSH for cold-shock resistance "by chance" modifies the developmental pathway for the color-pattern determination on the wing. This model also points out the existence of an evolutionary physiological constraint at the genus level, an example of genetic assimilation of phenotypic plasticity, a possible molecular basis of the classic allopatric speciation model, and the importance of the pupal stage in insect evolution. Although the generality of this mode of evolution is uncertain, the physiological side-effect model could partly explain the existence of various non-functional or neutral morphological features in butterflies and other organisms. Experimental identification of the putative CSH and subsequent examination of correlation between the CSH level and color patterns are expected in the future.

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摘　　要

非機能性形質あるいは中立的形質の多様化のための生理的副作用モデル: アカタテハ属の進化史に関する考察 (大瀧丈二)

チョウの翅の色模様 (色彩パターン) は非常に多様である. 多くの色模様あるいはそのエレメントは, 交

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配, 擬態, 隠蔽などにおいて生態的, 行動的な機能を持つが, それらのすべてが明確に特定できる機能を持っているわけではないと考えられる. どのようにして, そのような機能を持たない, 時には浪費にも思われるような色模様形質が進化したのか, 現在のところ謎となっている. そのような過程を明確化するため, 狭義のアカタテハ属の色模様進化のモデルを提案する. 最初に, アカタテハ属の祖先種は温度変化の激しい高地に地理的に隔離されたと考える. このモデルでは, 温度変化に反応して, 分化途上の細胞を保護するために蛹は冷却ショックホルモンを分泌する. このホルモンは, 副作用あるいは多機能効果として, 翅の色模様を修飾する偶発的な能力を持つ. そのことにより, 祖先種の表現型可塑性が表出される. しかし, 修飾された表現型に適応性があることは稀である. ほとんどの場合は, 交配に不都合なものにすぎないか, 特に悪影響も適応性もなく中立的なだけである. しかしながら, 修飾された表現型は, 高ホルモン活性に対する自然選択に伴って起こる遺伝的同化の過程を通して, 集団内に固定されていく. 結果として, 高地に棲息する現存のアカタテハ属の翅における多様な橙色領域が生じる. このように, 冷却ショックホルモンは, 非機能的あるいは中立的な形質の遺伝的同化の触媒者として振舞う. 逆に言えば, 非機能的あるいは中立的な形質は, 冷却ショックホルモンなどの機能的形質に寄生するような形で集団中に広がり, 固定される可能性がある. 異所的種分化の古典的メカニズムが示しているように, 交配における嗜好性の進化に続いて交配前隔離が確立されたのだろう. この「生理的副作用モデル」は, アカタテハ属および他のチョウにみられる非機能的あるいは中立的な翅の色模様の多様性を説明することができると思われる.

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